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The absence of fire can cause a lag phase: The invasion dynamics of *Banksia ericifolia* (Proteaceae)

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Abstract The transition from a species introduction to an invasion often spans many decades (a lag phase). However, few studies have determined the mechanisms underlying lag phases. Such a mechanistic understanding is vital if the potential ecosystem-level impacts are to be predicted and the invasion risks to be managed proactively. Here we examine *Banksia ericifolia*, introduced for floriculture to South Africa, as a case study. We found 18 sites where the species has been planted, with self-sustaining (naturalized) populations at four sites, and an invasive population at one site. The invasion originated from around 100 individuals planted 35 years ago; after several fires this population has grown to approximately 10 000 plants covering about 127 ha. The current invasion of *B. ericifolia* already has ecosystem-level impacts, for example the nectar available to bird pollinators has more than doubled, potentially disrupting native pollination networks. If fires occurred at the other naturalized sites we anticipate populations would rapidly spread and densify with invaded areas ultimately become banksia-dominated woodlands. Indeed the only site other than the invasive site where fire has occurred regularly is already showing signs of rapid population growth and spread. However, recruitment is mainly immediately post fire and no seed bank accumulates in the soil, mechanical control of adult plants is cheap and effective, and immature plants are easily detected. This study is a first in illustrating the importance of fire in driving lag phases and provides a valuable example for why it is essential to determine the mechanisms that mediate lag phases in introduced plant species. Serotinous species that have been introduced to areas where fire is suppressed could easily be misinterpreted as low risk species whilst they remain in a lag phase, but they can represent a major invasion risk.

Key words: biological invasion, early detection and rapid response, eradication, fynbos, horticulture, Proteaceae, time lag.

INTRODUCTION

Once a species becomes established in a new region considerable time may pass before there is a noticeable increase in the population size (Baker & Stebbins 1965; Kowarik 1995; Crooks 2005). Population growth rates during biological invasions often show an inflection point (Shigesada & Kawasaki 1997). Initially population growth rates are low (the so called lag phase), then, following some trigger, population growth rate is higher and range expansion occurs much more rapidly. The phenomenon of lag phases is increasingly recognized as an integral part of many invasions (Sakai *et al.* 2001; Aikio *et al.* 2010). Despite this, and the considerable research effort directed at the mechanisms that drive invasions, there are very few empirical data on the mediators of lag phases (Pyšek & Hulme 2005; Lockwood *et al.* 2007; Larkin 2012). Potential triggers that have been suggested to facilitate an invasion many years after introduction include climate changes (Kowarik 1995), the opening up of safe sites for germination (Harper 1977), genetics (Baker & Stebbins 1965), shade tolerance (Wangen & Webster 2006), and intraspecific interactions such as the Allee effect or removal of herbivores (reviewed in Crooks 2005). However, understanding what drives lag phases is crucial for effective management of invasive species; without this managers are likely to make erroneous risk assessments and miss critical windows for action (Crooks 2005).

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Species with a long lag phase between introduction and spread can also create substantial conflicts of interest. Intentionally introduced species might be used for a long time and become widely utilized and accepted. However, the initial benefits are often surpassed by negative impacts when the species becomes invasive, leading to some species becoming net costs in a country (Ewel *et al.* 1999; De Wit *et al.* 2001; McNeely 2001; Shackleton *et al.* 2007; van Wilgen *et al.* 2011; Wise *et al.* 2012). The fact that many introduced plant species with some initial value are introduced for agriculture, forestry and the horticultural trade (Wells *et al.* 1986; Prescott Allen & Prescott Allen 1990; Evans 1992; Dehnen-Schmutz *et al.* 2007a,b; Richardson 2011) is problematic because the initial beneficiaries are rarely willing or able to carry the costs associated with remediating invasions; consequently, these become a public cost (McNeely 2001). Therefore, predictive and proactive management approaches are required that are sensitive to the value of any introduced species (Wilson *et al.* 2011). Once a valuable introduced species is well established and found to pose a risk, eradication is likely to be extremely costly or impossible. In order to minimize public costs, proactive management at an early stage of invasion is essential (Rejmánek & Pitcairn 2002).

South Africa has a long history of dealing with introduced and invasive plants that have caused a variety of impacts (e.g. reducing native species richness and threatening scarce water resources (Richardson & van Wilgen 2004; Gaertner *et al.* 2009)). Australian species are well represented among the most widespread and damaging invasive species in South Africa (Henderson 2006). This is particularly evident in the fynbos biome where the dominant invasive species are trees and shrubs that originated from environmentally similar regions in Australia, including several species of Proteaceae from the genus *Hakea* (Richardson *et al.* 1987, 1992). Another Australian genus of proteas, *Banksia*, has very similar life-history traits and environmental requirements to *Hakea*, and several species in the genus have been identified as posing a high risk of becoming major invaders (Richardson *et al.* 1990).

Over the last few decades at least 14 *Banksia* species have been introduced to the fynbos areas of South Africa, mainly for the cut-flower industry (floriculture). *Banksia ericifolia* L.f. is the most-widely planted of these species (Protea Atlas Project database, http://protea.worldonline.co.za; S. Geerts, 2011, pers. obs.). Two geographically distinct subspecies of *B. ericifolia* are recognized: *B. ericifolia* ssp. *ericifolia* and *B. ericifolia* ssp. *macrantha* (Taylor & Hopper 1988); only the former is used in horticulture in South Africa. This species was identified as one of the banksias most likely to become invasive in South Africa (Richardson *et al.* 1990, 1997; Hönig *et al.* 1992). While the species is not currently listed as invasive under South African legislation, it would fail a pre-border weed risk assessment (Appendix S1, Pheloung *et al.* 1999; Hawaii Pacific Weed Risk Assessment 2012).

Because lag times can vary in length (Kowarik 1995; Aikio *et al.* 2010) it can be very difficult to determine whether there will be substantial costs arising from a future invasion. Therefore, detailed information on specific systems is required to improve the understanding and predictability of lag phases. Here we provide an assessment of the mechanisms for an observed lag phase, using a floricultural tree in South Africa, *B. ericifolia*, as a case study.

METHODS

Study species

Banksia ericifolia is well adapted to grow in nutrient-poor soils, characteristic of large parts of Australia (Orians & Milewski 2007) and southwestern parts of South Africa (Cowling 1992). The species is also fire-adapted with winged seeds stored in protective wooden follicles (Bradstock & Myerscough 1981). Follicles are clustered on a flowering spike to form an infructescence that is retained in the canopy (serotiny) (Cowling *et al.* 1989; Lamont *et al.* 1991). Fire is necessary to rupture these follicles and release the seeds in the competition free, post-fire environment (Zammit & Westoby 1988). Recovery after fire only occurs from seeds, which can result in high density almost mono-specific stands (Siddiqi *et al.* 1976; Bradstock & Myerscough 1981; Morris & Myerscough 1988). Individual plants take approximately 5 years before they start flowering in the native range (Bradstock & O'Connell 1988; Morris & Myerscough 1988) whilst in South Africa plants appear to flower as early as 3 years (Hönig *et al.* 1992).

Being an obligate seeder, high reproductive output is essential for the establishment of *B. ericifolia* (Carpenter & Recher 1979). However, as in most other *Banksia* species (Collins & Rebelo 1987; Carthew *et al.* 1996; Goldingay & Carthew 1998), autonomous seed production in *B. ericifolia* is low (Goldingay *et al.* 1991). Low levels of self-compatibility are not typically associated with invasiveness (Rambuda & Johnson 2004) but banksias are expected to find reliable pollinators in South Africa because of the similarities between Australia and South Africa in nectar-feeding bird pollinators (Collins & Rebelo 1987; Le Roux *et al.* 2010), which are well adapted for utilizing novel nectar sources (Geerts & Pauw 2009).

Banksia ericifolia has been planted outside its native range in Europe (Cullen *et al.* 2000), Hawaii (St. John 1973), New Zealand (where it is recorded as naturalized (Randall 2002; Howell & Sawyer 2006; GBIF 2011)), Réunion Island (although it is apparently no longer present there (C. Lavergne, 2010, pers. comm.)), and South Africa. The earliest *B. ericifolia* records in South Africa are from the 1970s when it was first planted as a floricultural species (A. Brink, 2011, pers. comm.), with the first records of naturalization in the mid-1990s (Richardson *et al.* 1997).

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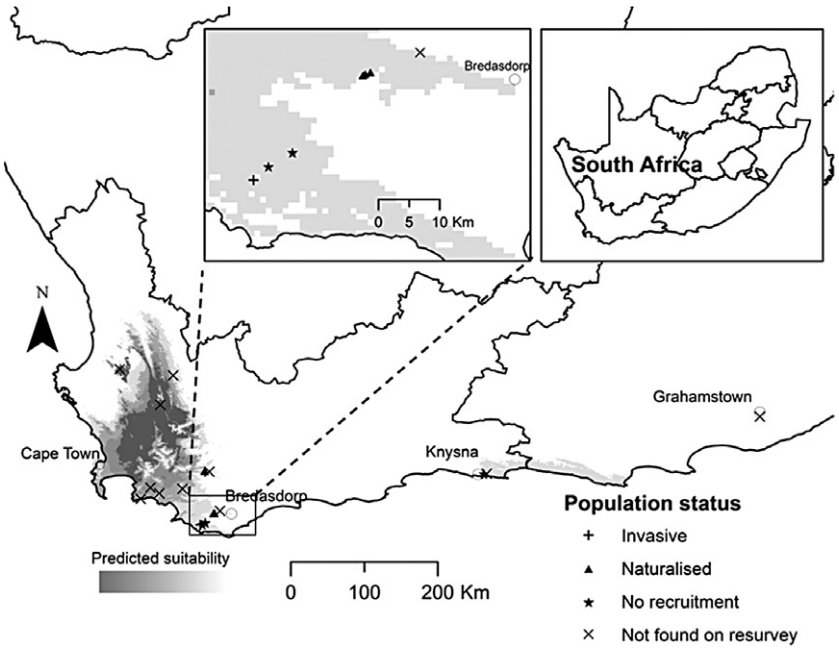

Fig. 1. Map of *Banksia ericifolia* records in South Africa showing climatically suitable areas based on bioclimatic analysis using locality records from the native range.

Study sites

The stimulus for the study was the report from South African National Parks of a *B. ericifolia* population in land recently acquired as part of extending the Agulhas National Park (Waterford section). To determine whether the species showed signs of spreading at other sites, a list of all *B. ericifolia* records in South Africa was compiled from the Protea Atlas Project database (Rebelo 1991, Rebelo 2001), the Southern African Plant Invaders Atlas (SAPIA) (Henderson 1998), iSpot (http://www.ispot.org.za/) and field visits to South African flower farms that grow Australian Proteaceae. Farmers were also questioned about potential localities and other flower farms producing banksias currently or in the past. All localities from the compiled list were visited between 2010 and 2012 to determine presence and naturalization or invasion of *B. ericifolia* (Appendix S2, Fig. 1). The invasion status of sites was classified according to Pyšek *et al.* (2004) and Blackburn *et al.* (2011).

Age distribution allometry and reproductive output

Each plant found was measured and mapped. Mapping involved walking parallel transects 5–10 m apart through the population. Large trees are highly visible from a distance but for seedlings a searching distance of at least 30 m past the furthest seedling was used. Searched areas are indicated in Figure 2.

To determine age structure, size at reproduction and total reproduction, several parameter were measured – height, canopy diameters at right angles, basal stem diameter, and number of inflorescences and mature cones. The significance of plant measurements in predicting the presence of reproductive structures was assessed using a generalized linear model with a binomial error distribution where the reproductive status was the response variable and height (log), mean basal diameter (log), mean canopy diameter (log) and site as predictor variables. The significance of plant size in predicting reproductive output was assessed using a linear regression model where the number of mature and open cones (log) was the response variable and similar predictor variables described above. Plants that were not reproducing were excluded from this analysis. To obtain seed number per cone, follicles of 67 cones from 12 trees of different sizes were examined. Using an allometric relationship derived between size and reproductive output, and the estimate of the number of seeds per cone, the size of the aerial seed-banks at each site was estimated.

The current occupied area was calculated using convex hull polygons based upon the Graham's scan algorithm in Arc-GIS 10. To estimate the rate of spread at Waterford, aerial photographs and Google earth images were used to determine when adult *B. ericifolia* plants occurred outside the original plantings. All plants at the Waterford site were cleared in April 2010 (except approx. 20 plants used for pollinator observations in this study). Adult trees were cut at ground level and seedlings were hand-pulled. At McGregor all seedlings were pulled and resprouting adult plants cut. At all other sites no plants were removed.

Reproductive ecology

Banksia ericifolia depends on pollinators for seed production and seeds for persistence. To determine the identity of

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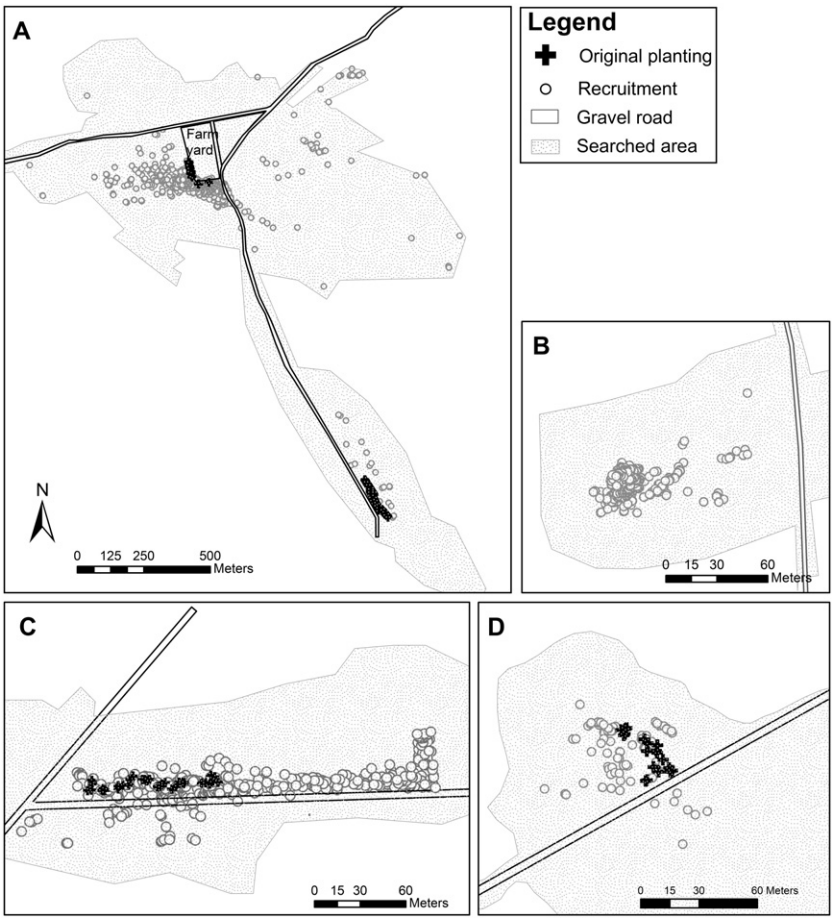

Fig. 2. Distribution of the four *Banksia ericifolia* study populations in South Africa: (A) Waterford in the Agulhas National Park; (B) McGregor; (C) young Blomkloof unburnt population (planted in the 1990s); (D) old Blomkloof unburnt population (planted in the 1970s). At Waterford, plantings south of the farm house were removed a few years prior to this study and only three of the approximately 20 stumps remained. Original planting details for McGregor are unknown. Grey dotted areas denote searched areas, see text for details.

pollinators, flowers were observed during the mornings and the afternoon at two sites (Waterford: 25 April, 4 May and 26 May 2011, for 470 min in total; Blomkloof: 13 July 2011 for 310 min). For all pollinators, visitation rates were quantified as visits per inflorescence per hour. At Blomkloof nocturnal observations, using LED lights and a camcorder fixed on night shot (12 and 13 July 2011 174 min in total), were made. Thirty-six rodent traps were placed out at dusk of the nights of 12–14 July 2011. These were baited with peanut butter and tuna, and placed at ground level close to inflorescences. Snouts of trapped rodents were swabbed with Fuschin gel and pollen loads were examined under a light microscope.

To estimate nectar production at the Blomkloof population, we sampled inflorescences using a 10 μL capillary tube and sucrose concentration with a 0–50% field handheld refractometer. As banksias have hundreds of densely arranged flowers on an inflorescence (Armstrong & Paton 1990), we sampled 10 evenly spaced flowers from one randomly selected column. Six inflorescences were sampled every 2 h throughout the day. In addition, eight inflorescences were bagged for 12 h to estimate nectar accumulation. Inflorescences were selected from plants of the same size and with a similar proportion of open flowers (50–80%). Nectar was converted to milligrams of sucrose per flower and total amount of sucrose produced per inflorescence extrapolated from these data. The number of flowers was calculated using the regression equation of Paton and Turner (1985). To determine ecosystem level impacts, sucrose availability was compared with similar aged native Proteaceae vegetation (Geerts 2011).

Dispersal

As a rough estimate of dispersal, we surveyed seedlings around two isolated post-fire adult plant skeletons (nearest neighbours were >120 m) at Waterford. As no seedlings were encountered further than 30 m from adults and the maximum seed dispersal range is known to be 48 m, a

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50 m search radius was used (Hönig *et al.* 1992). The seedling shadow was estimated based on frequency density plots (function dist in R).

Post-fire seed and seedling density

To estimate post-fire seed density, seeds in a dense part of the Waterford population were counted along two 50×5 m transects (4 months after the fire most seeds were released from the cones and were clearly visible on the soil surface). Post-fire seedling density was measured along a 2-m-wide transect through the densest parts of the population (May 2011). The transect extended through the population until no more seedlings were found (at least 30 m past the last seedling). The same method was followed in a demarcated part of the population (between a road and fence) where surviving and dead plants were mapped and measured in full after the fire. For the smaller McGregor population, all seedlings were counted.

Soil seed bank, seed viability and resprouting

While no soil seed-bank has been observed in the native range (Jenkins *et al.* 2010), we did a brief check of this. Areas with the highest density of seedlings (>10 m^{-2}) and seeds (>100 m^{-2}) on the soil surface at Waterford were selected. Two plots of 25×25 cm by 20 cm deep were dug, and the soil sieved for seeds. To test for seed viability, seeds ($n = 49$) were collected from open cones at Waterford, and respiration tested using a standard tetrazolium test (Peters 2005).

To assess the ability of plants to resprout we monitored plants for their potential to resprout 1.5 years after fire and clearing at Waterford. Basal stem diameter of all resprouting plants was measured ($n = 378$). Resprouting was also assessed for all plants at McGregor.

Bioclimatic analysis

A bioclimatic analysis was based on native distribution records sourced from the Atlas of Living Australia (http://www.ala.org.au, accessed May 2012). After data cleaning (missing coordinates, spatial uncertainty, points in the ocean and duplicated locality points were removed), 393 records remained. We used the Köppen-Geiger vegetation mask to define the background for the model (dismo package, Hijmans *et al.* 2012). Twelve thousand pseudo-absence points were then created within which one or more presences occur (Barbet-Massin *et al.* 2012). Environmental data at 30 arc second resolution were sourced from the WorldClim database (http://www.worldclim.org, accessed June 2012). To limit colinearity we used the four variables with the lowest pairwise correlations (Kendall rank correlation coefficient < 0.6): temperature seasonality, mean temperature of the coldest quarter, precipitation of the coldest quarter and total range in mean monthly precipitation. The model was generated from three algorithms within the BIOMOD package (Thuiller *et al.* 2009) implemented in R 2.15.1 (R Development Core Team 2009): generalized additive models (GAM, Hastie & Tibshirani 1990); artificial neural networks (ANN, Ripley 1996) and generalized boosted models (GBM, Ridgeway 1999), calibrated using 70% of the initial data and then evaluated on the remaining 30%. Model accuracy was analysed using the average true skill statistic (TSS, Allouche *et al.* 2006), and area under the receiver operating characteristic curve (AUC, Hanley & McNeil 1982).

RESULTS

Population history, fire regime and invasiveness

Of the 11 Protea Atlas and two SAPIA records, only two *B. ericifolia* populations still exist (though the Protea Atlas treated the two original sites of plantings at Waterford as separate populations, Fig. 2A). In addition, we identified six new populations from the field visits and consultations with local landowners (Appendix S2, Fig. 1). We recorded four naturalized populations but no invasive populations other than the original report received from the Waterford section of the Agulhas National Park.

The invasive population arose from about 20 plants planted as a hedge around a farmyard and approximately 80 plants planted in a twin-aisled grove along a road, presumably intended for flower production. Both are believed to have been planted in the early 1980s. From aerial photographs and Google Earth (Google 2012) there was no indication of large adult plants outside the farmyard or planted grove prior to the farm ceasing commercial activity in 2002, despite parts of the area burning in 1990 and 1996/1997. In December 2005 and 2009 most of the population burnt. Two cohorts visible in the size frequency distributions (Fig. 3) were almost certainly caused by pulses of recruitment following these fires. After the December 2009 fire, the population consisted of a number of tall, mature trees that survived the fire close to the farm-house, many burnt skeletons further away, and a dense carpet of seedlings extending over 126.7 ha (Fig. 4a).

The other populations where naturalization was evident occupied a much smaller area and had less recruitment (Fig. 2B–D). The older Blomkloof population was of similar age to Waterford, but was the smallest (0.18 ha in extent), while the younger Blomkloof population covered about 1 ha (Appendix S2). At Blomkloof, the limited recruitment observed was likely facilitated by the regular disturbance of surrounding land (Appendix S3), but both populations have been protected from fire (A. Brink, 2011, pers. comm.). The McGregor population arose from seven planted individuals (Protea Atlas Project),

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but increased to 207 plants after a fire in 1999 and to 2428 seedlings, covering 0.3 ha, after a fire in 2009 (Appendix S2).

Age distribution allometry and reproductive output

The single best predictor of reproductive onset was basal diameter (approx. 77.0% of the deviance). A model with height alone had less explanatory power but still explained 71.3% of the deviance (Appendix S4, Fig. 5). For size at onset of reproduction there was a weak effect of site, but this was likely due to the length of time since the last fire and the time of year when we sampled.

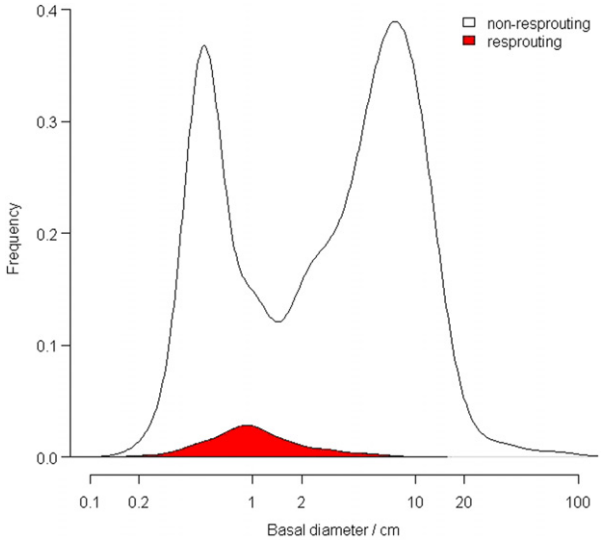

Fig. 3. Frequency distribution of resprouting (and non-resprouting) *Banksia ericifolia* individuals (Waterford only). The first peak is the seedling cohort (2009 fire) and the second peak the cohort from the previous fire (2005 fire). The potential for small plants to resprout is underrepresented since small individuals were hand pulled rather than cut.

For size versus reproductive output, the single best predictor was again basal diameter (Appendix S4). There were no significant differences in number of follicles per cone between trees (Appendix S4) and an average follicle value of 65.2 (± 22.0, 1 SD) was used in further calculations. *Banksia ericifolia* plants produce mature cones at about 1 m tall (Fig. 6), but production rises exponentially with height thereafter. For large individuals, a massive seed load is carried in the canopy, with total cone production the highest at Waterford (38 332 040) followed by the unburnt populations (Blomkloof old, 648 440; Blomkloof young, 1 098 240) with the McGregor population containing the lowest number of cones (368 030)

Reproduction

Birds and insects were frequently observed visiting *B. ericifolia* flowers (Fig. 4b, Appendix S5). While no rodent visitation was observed, captured rodents carried pollen loads on their snouts (two *Rhabdomys pumilio* had 17 and 150, and one *Mus minutoides* 3 pollen grains). There was no significant difference in *B. ericifolia* nectar standing crop throughout the day (Kruskal–Wallis $H = 4.87$, d.f. = 7, $P = 0.68$; Appendix S6), so data were pooled. The average volume of nectar per inflorescence was 672.7 µL (95% CI = 519.3–826.1), with an average sucrose concentration per flower of 26.1 (95% CI = 23.4–28.8). From these values an ecosystem level comparison was possible, with total sucrose at Blomkloof more than double (7152 g ha^{-1}.) that of similar aged native Proteaceae vegetation (2683 g ha^{-1}; average of 7 localities (Geerts 2011)).

Dispersal

Most seedlings occurred within 10 m of adult plants (95% and 55% for the two individuals studied). In

Fig. 4. (a) After fire a dense carpet of seedlings of *Banksia ericifolia* dominates the new growth. (b) Cape Sugarbird (*Promerops cafer*) pollinating a *B. ericifolia* flower. (c) Plants with small basal diameters can resprout even if cut close to ground level.

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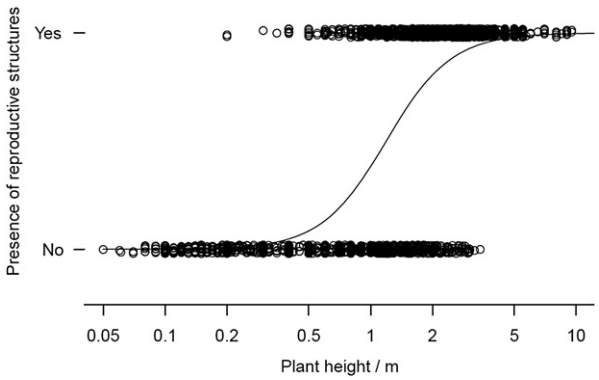

Fig. 5. The relationship between height and reproductive maturity in *Banksia ericifolia*. The line shown is from a fitted generalized linear model with binomial errors and plant height as an explanatory variable.

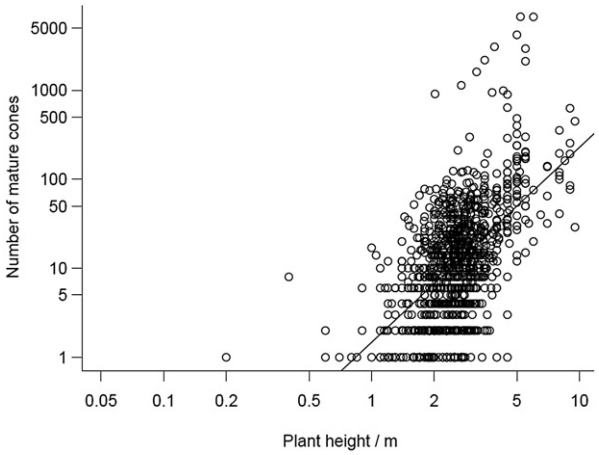

Fig. 6. The relationship between reproductive output [log (number of mature or open cones)] and the number of cones per plant [log (plant height, cm)] in *Banksia ericifolia*.

total, less than 2% of seedlings occurred further than 20 m from an adult plant, with a maximum effective dispersal distance of 30 m (Appendix S7). Dispersal direction and distance were not discernibly related to wind direction in the post-fire environment.

Post-fire seed and seedling density

Post-fire seed density in the densest part of the Waterford population averaged 47 ± 8.3 (95% C.I.) seeds per square meter, with an average seedling density of 32 ± 17.5 (95% C.I.) per square meter a year later (Fig. 4a). In the demarcated area of 680 m^2 there were 127 plants before the fire, with heights ranging from 1.3–4.1 m, and a total of 2828 seedlings after the 2009 fire. Post-fire seedling density at McGregor was 0.82 seedlings per square metre (2428 seedlings over 2954 m^2).

Soil seed bank, seed viability and resprouting

All seeds were found on top of the leaf litter, and no seeds were found in the soil. All tested seeds were viable ($n = 49$). There was no evidence that large trees resprouted. At Waterford smaller plants (basal diameter 1–97 mm, Fig. 3) did resprout (Fig. 4c). At McGregor only 4 (out of the 207-burnt plants) resprouted, with basal diameter ranging from 47–85 mm.

Bioclimatic analysis

Calibrated models show a good predictive power of species distributions (AUC > 0.95 for all models and TSS > 0.8 for all models; Appendix S8). Bioclimatic projections reveal that around 21% of the Western Cape of South Africa is highly to moderately suitable for *B. ericifolia* (Fig. 1).

DISCUSSION

Understanding the mechanisms responsible for lag phases of introduced species is important, both for the advancement of robust theories and models in invasion ecology and for informing management. For example, the absence of buzz pollinators prevented certain legumes from invading Tasmania; subsequent introduction of bees stimulated recruitment and spread (Stout *et al.* 2002). Here we show for the first time that natural fires influence lag phases in alien species. Regular fires acted as the stimulus for invasion of *B. ericifolia*, an invasion that had been predicted to be likely, based on an analysis of species traits (Richardson *et al.* 1990).

Banksia ericifolia was present in South Africa for over four decades without becoming invasive despite large areas of the south-western part of the Western Cape being climatically suitable, and no apparent reproductive limitation (indeed populations have built up massive canopy-stored seed-banks). However, populations can expand rapidly if burnt, for example at Waterford. Simulations show that even with only a single fire occurrence in the next decade populations are likely to increase significantly in area occupied (Appendix S9).

In the absence of fire, populations remain in a lag phase since populations older than 20 years release sufficient propagules to sustain a naturalized population, but establishment and spread is low (Bradstock & O'Connell 1988; Zammit & Westoby 1988). In contrast, population expansion will be rapid after fire. For example, two fire cycles at McGregor have seen the population expand from approximately 7 plants in 1999 to a few thousand seedlings covering 0.3 ha a

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decade later. The current general increase in natural fire frequencies will likely favour *B. ericifolia* invasions (Cowling 1992; Bond & Van Wilgen 1996). At populations under active management and protected from fire (e.g. at Blomkloof), occasional seedlings recruiting outside plantations could serve as new invasion foci. Although most recruitment is within 30 m (Appendix S7), and dispersal range is known to be 48 m (Hönig *et al.* 1992), some individuals in this study occurred at greater distances, suggesting rare long-distance dispersal events (Pergl *et al.* 2011). Such longer-distance dispersal events are hugely important in driving rapid range expansion and population growth in invasive species, as has been demonstrated for other woody invasive plants in fynbos (Higgins & Richardson 1999).

Many of the dominant alien invasive species in the fynbos biome are fire-adapted trees without close analogues in the fynbos (Richardson *et al.* 1992). However, there are many native proteas similar in growth form and habit that compete for the same niche as *B. ericifolia* (Hönig *et al.* 1992). Consequently, besides the usual attributes such as release from natural enemies, a history of cultivation and climatic suitability, other factors might have contributed to the invasion success of *B. ericifolia*. Firstly, *B. ericifolia* has a higher growth rate than other banksias and native South African Proteaceae (Morris & Myerscough 1988; Hönig *et al.* 1992). Second, their ability to produce seeds at a younger age (4 years) than most Proteaceae is a major advantage in a fire-prone environment (Hönig *et al.* 1992), particularly with an increase in fire frequencies (Cowling 1992; Bond & Van Wilgen 1996). Third, they have large seed production, up to a hundred times more than co-occurring banksia species in Australia (Carpenter & Recher 1979) and native South African Proteaceae (Maze & Bond 1996). Lastly, *B. ericifolia* is not influenced by the *Phytophthora cinnamomi* fungus, unlike other *Banksia* species in Australia and native *Protea* species in South Africa (McCredie *et al.* 1985; Von Broembsen & Brits 1985).

Our results show that *B. ericifolia* more than doubles the amount of nectar per hectare when compared with native Proteaceae species in fynbos. This additional nectar resource is utilized by a large variety of floral visitors, to the extent that pollinator visitation rates in South Africa are almost six times that in the native range (1.15 *vs.* 0.19 visits per inflorescence per hour; Paton & Turner 1985), largely due to the honeybee, *Apis mellifera*. Honeybees are known to increases *B. ericifolia* seed production in parts of Australia where they were introduced (Paton & Turner 1985). The influence of this large additional nectar source on the native pollinator community and their dependant plants remains to be tested, but high *A. mellifera* densities have been shown to decrease bird visitation rates in South Africa (Geerts & Pauw 2011).

Fortunately, *B ericifolia* is relatively easy to control. Plants have no thorns and are not toxic and no persistent seed bank accumulates in the soil. Herbicide is not required to prevent large plants resprouting, but small plants, for which there are still active meristems close to the ground, require additional attention or follow-ups to deal with resprouting (Fig. 3). Currently, there is little demand for *B. ericifolia* in the cut-flower industry and no new plantations are considered (A. Brink, 2011, pers. comm.). At a relatively low cost of 59 642 ZAR (cost for study, assessing and clearing the approx. 10 000 individuals at Waterford) for clearing the only invasive population, removal and monitoring the remaining populations is a feasible option. Based on the evidence provided here, *B. ericifolia* could be regulated by area, whereby a demarcation permit is required and plants may only be grown under controlled conditions. Alternatively, if no objections are raised, a nation-wide eradication plan should be implemented.

In summary, our results suggest that fire regime and lack of management might ultimately govern invasion of *B. ericifolia*. Ecological studies of this type are needed to elucidate the underlying mechanisms behind invasions. We showed that with detailed data we could infer the point at which the lag phase terminated for *B. ericifolia* retrospectively. Although there is some scepticism about the usefulness of this approach (Groves 2006), we show that if it is still fairly recent after the inflection point, eradication is still feasible.

Invasions of *B. ericifolia* in other regions of the world are also likely to be limited by fire regime (but unlikely to be limited by pollinators). The invasion risk of *B. ericifolia*, used for floricultural production, can be minimized if populations are recorded, monitored and fairly simple contingency plans put in place (i.e. abandoned plantations are removed). Given the long establishment phase and the specific triggers for invasions, one of the greatest risks associated with serotinous exotics might be underestimating their potential as successful invaders.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Assessment of the potential invasiveness of *Banksia ericifolia* in South Africa.
Appendix S2. All records of *Banksia ericifolia* in South Africa.
Appendix S3. Distribution of plant heights at each population.
Appendix S4. Parameters that predict reproduction.
Appendix S5. Pollinator visitation rates.
Appendix S6. Nectar standing crops of *B. ericifolia* inflorescences.
Appendix S7. Seedling distribution around two isolated adult plant skeletons.
Appendix S8. Climate model fit.
Appendix S9. Current and projected areas occupied.

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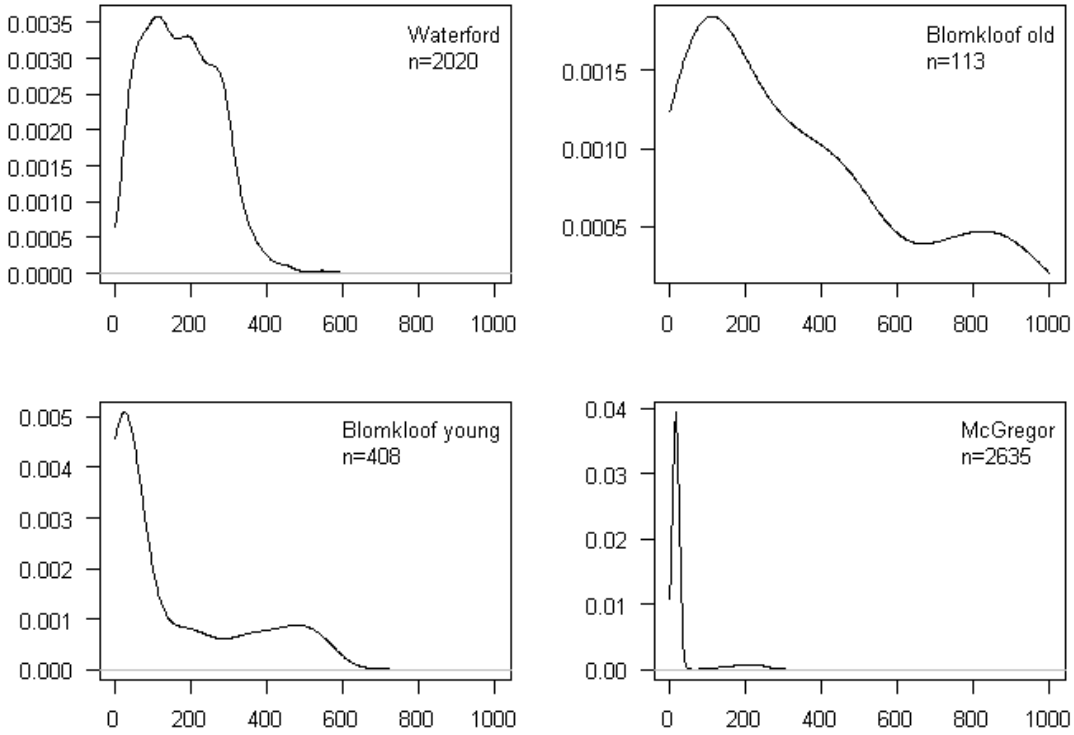
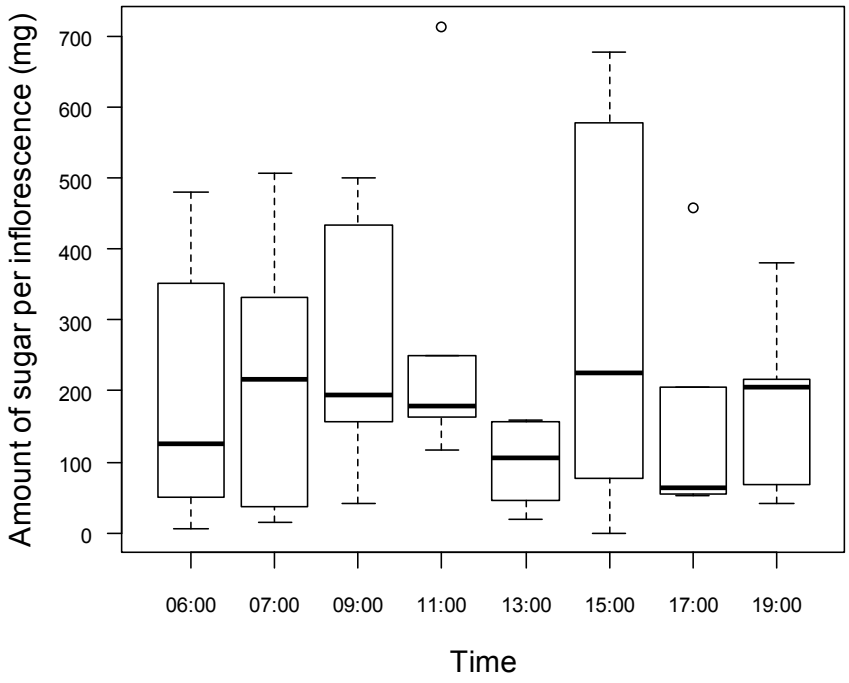
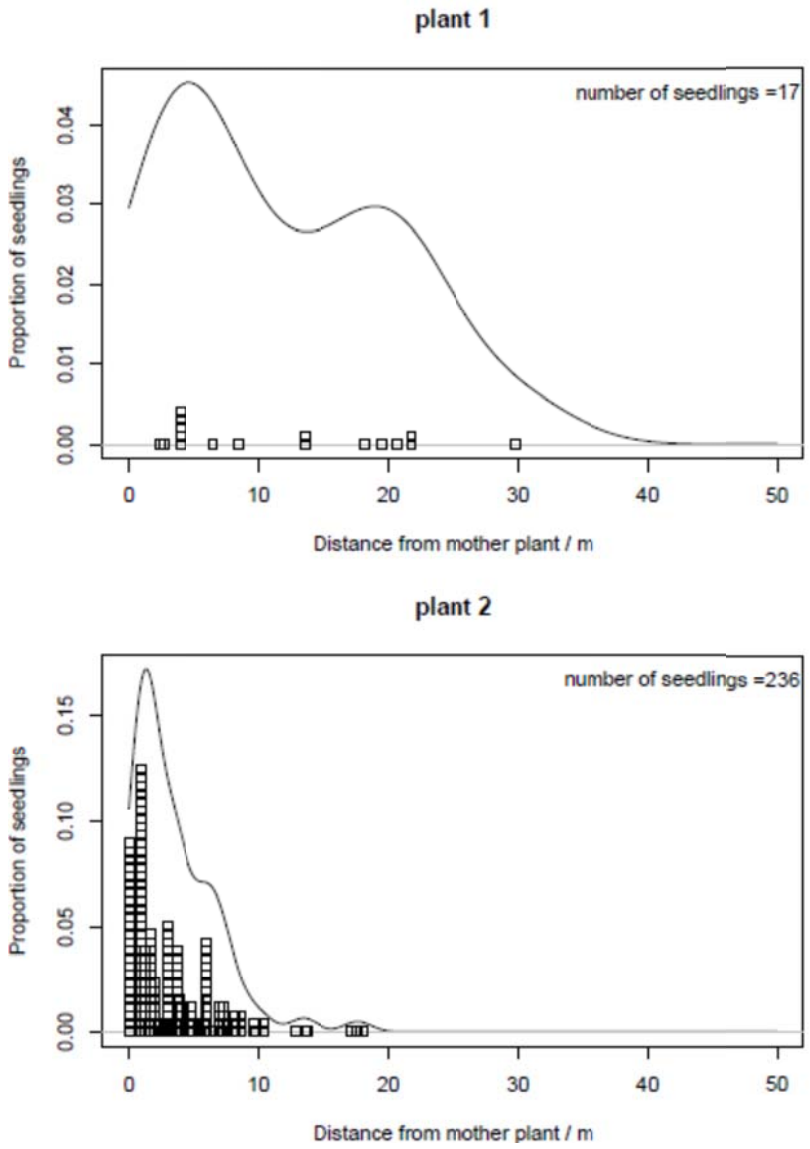
Supplementary Figure 1



Supplementary Figure 2



Supplementary Figure 3



Supplementary Table 1. We assessed the potential invasiveness of *Banksia ericifolia* in South Africa by using the Australian Weed Risk assessment protocol of Pheloung et al. (1999). Total score for *B. ericifolia* in South Africa is 9. For list of references see the Hawaii Pacific Weed Risk Assessment (HPWRA) for *B. ericifolia* (Hawaii Pacific Weed Risk Assessment 2012).

Question	**Answer**
Is the species highly domesticated?	No
Species suited to South African climates	High.
Quality of climate match data	High
Broad climate suitability (environmental versatility)	Yes
Native or naturalised in regions with extended dry periods	Yes
Does the species have a history of repeated introductions outside its natural range?	Yes
Naturalised beyond native range	Yes
Garden/amenity/disturbance weed	No
Weed of agriculture/horticulture/forestry	No
Environmental weed	
Congeneric weed	Yes
Produces spines, thorns or burrs	No
Allelopathic	No
Parasitic	No
Unpalatable to grazing animals	
Toxic to animals	No
Host for recognised pests and pathogens	No
Causes allergies or is otherwise toxic to humans	No
Creates a fire hazard in natural ecosystems	Yes
Is a shade tolerant plant at some stage of its life cycle	
Grows on infertile soils	Yes
Climbing or smothering growth habit	No
Forms dense thickets	Yes
Aquatic	No
Grass	No
Nitrogen fixing woody plant	No
Geophyte	No
Evidence of substantial reproductive failure in native habitat	No

Produces viable seed	Yes
Hybridizes naturally	
Self-compatible or apomictic	Yes
Requires specialist pollinators	No
Reproduction by vegetative propagation	No
Minimum generative time (years)	3
Propagules likely to be dispersed unintentionally	No
Propagules dispersed intentionally by people	Yes
Propagules likely to disperse as a produce contaminant	No
Propagules adapted to wind dispersal	Yes
Propagules water dispersed	No
Propagules bird dispersed	No
Propagules dispersed by other animals (internally)	
Propagules dispersed by other animals (externally)	No
Prolific seed production (>1000/m2)	Yes
Evidence that a persistent propagule bank is formed (>1 yr)	Yes
Well controlled by herbicides	
Tolerates or benefits from mutilation, cultivation or fire	No
Effective natural enemies present	

Supplementary Table 2. All records of *Banksia ericifolia* in South Africa including current and extinct populations. The planting date is unknown for most populations.

Locality	Number of plants (previously recorded)	Number of plants (as observed in this study)	Area covered in 2010 (hectares)	Status[1]	Year planted	Latitude	Longitude	Detailed description
Waterford, Agulhas	Waterford 100-10000* Wolvegat 10-100*	9401 (before 2009 fire)	126.7	D2	1977	19.64833	-34.68333	Waterford 314 / Koksriver 313 / Wolvengat
McGregor 1	7 *	207 (before 2009 fire) 2428 (after)	0.3	C3		19.70167	-34.00800	Onverwacht Protea orchard on a farm outside McGregor. bordering the Cape Nature Riviersonderend Mountain catchment area
Kleinmond	10#	0		Was C3 now †		19.15000	-34.28333	Honingklip farm. Plants eradicated
Blomkloof	0	121	0.18	C3	1977	19.82022	-34.52328	Blomkloof farm, old population
Blomkloof	0	793	0.98	C3	1998	19.81258	-34.52572	Blomkloof farm, young population
Blomkloof	0	~50	0	C3	1998	19.80912	-34.52785	Blomkloof farm mixed Banksia hedge
Grabouw	Not indicated*	0	0	B3		19.04150	-34.21050	Jutland Farm 452. South of Grabouw
Napier	Not indicated*	0	0	B3		19.89333	-34.49550	Shooting range at Napier Farm142
Bettys bay	3*	0	0	B3		18.92333	-34.35000	400 meters West of Dawidskraal bridge
Citrusdal	2*	0	0	B3		19.31950	-32.83567	Langerivier 120. 40km South east of Citrusdal
Grahamstown	2*	0	0	B3		26.49950	-33.34050	Brackendal at Grahamstown
Caledon	2#	0	0	B3		19.43277	-34.22694	N2 inland road verge between two entrances to Caledon
Knysna	10-100*	0	0	B3		23.15483	-34.04183	Ryk Haupht farm at Knysna
McGregor 2	10-100*	0	0	B3		19.76183	-34.01683	Derietvalley 154.Experimental planting. Population died through natural causes.

Tulbagh	1*	0	0	B3		19.16283	-33.19550	Straatskerk 190 at Tulbagh
Piketberg	1*	0	0	B3		18.66567	-32.75983	Tweefontein 81 at Piketberg. Hedge according to iSpot (2002 record). Cut down between 2002 and 2011.
Knysna	0	1	0	C1	2000	23.11529	-34.04165	Knysna
Elim	0	474	0.51	C1	2001	19.70539	-34.64081	Viljoenshof close to Elim at Agulhas
Elim	0	16	0.01	C1	2001	19.66998	-34.66166	Hedge on property adjoining Viljoenshof

[1]Categorisation according to Blackburn (2011) framework:

B3: Individuals transported beyond limits of native range, and directly released into novel environment

C2: Individuals surviving in the wild in location where introduced, reproduction occurring, but population not self-sustaining

C3: Individuals surviving in the wild in location where introduced, reproduction occurring, and population self-sustaining

D2: Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction.

Supplementary Table 3. Size parameter important in predicting the onset of reproduction and the reproductive output

Size vs. onset of reproduction

Model terms	ΔAIC	df	weights
b + c + h + s	0.0	7	0.970
b + c + s	7.0	6	0.029
b + c + h	29.8	4	<0.001
b + h + s	30.0	6	<0.001
b + s	67.4	3	<0.001

b is *log (mean basal diameter)*

c is *log (mean canopy diameter)*

h is *log (height)*

s is s*ite*

Parametric coefficients:	Estimate	Std. Error	t value	Pr(>|t|)
Intercept				
Site blomkloof old	-14.0288	1.4705	-9.54	< 2e-16
log(canopy)	1.672	0.2295	7.286	3.20E-13
log(banksia$ht)	0.8387	0.2867	2.925	0.00344
log(basal diameter)	1.0145	0.1854	5.473	4.43E-08
Site blomkloof young	0.8668	0.511	1.696	0.08981
Site McGregor	2.0689	0.4613	4.485	7.30E-06
Site Waterford	0.8593	0.418	2.056	0.03982

Null deviance: 4789.1 on 4563 degrees of freedom

Residual deviance: 1101.7 on 4557 degrees of freedom

AIC: 1115.7

Size vs. reproductive output

Model terms	ΔAIC	df	weights
b + c + s	0.0	7	0.723
b + c + h + s	1.9	8	0.277
b + h + s	75.7	7	<0.001
b + c + h	76.5	5	<0.001
b + c	79.1	6	<0.001

b is *log (mean basal diameter)*

c is *log (mean canopy diameter)*

h is *log (height)*

s is s*ite*

Parametric coefficients:	Estimate	Std. Error	t value	Pr(>|t|)
Intercept				
Site blomkloof old	-4.88	0.438	-11.1	< 2e-16
Log (canopy)	0.941	0.103	9.17	< 2e-16
Log (basal diameter)	0.988	0.0819	12.1	< 2e-16
Site blomkloof young	0.350	0.148	2.36	0.0185
Site McGregor	1.24	0.158	7.85	1.07E-14
Site Waterford	0.509	0.134	3.79	0.000163

Null deviance: 2058.26 on 995 degrees of freedom

Residual deviance: 866.92 on 990 degrees of freedom

This model explained ~57.9% of the deviance.

Details of models just using height

Formula: lm [*log* (*number of mature or open cones*) ~ *log (plant height in cm)*]

Parametric coefficients:	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	9.71	0.521	18.6	<2e-16
Log heights	2.19	0.0938	23.4	<2e-16

Residual standard error: 1.206 on 1107 degrees of freedom

Multiple R-squared: 0.3305, Adjusted R-squared: 0.3299

F-statistic: 546.4 on 1 and 1107 DF, p-value: < 2.2e-16

Cone size vs. number of seed-cases (Waterford only)

From a generalised linear mixed effects model using glmer[lme4] (tree as a fixed effect), there was no evidence of the number of cases differing for different sized plants. Comparing models with and without plant height: Chi-square $_{2,3}$ = 1.18, p = 0.2767.

Fixed effects	Estimate	Std. Error	*z*	P
Intercept	4.22078	0.05933	71.14	<0.0001
Tree				

Supplementary Table 4. Pollinator visitation rates to *Banksia ericifolia* inflorescences at Waterford and Blomkloof. (-)No visitation observed.

	Number of pollinator visits/inflorescence/hour	
Species	Waterford	Blomkloof
Orange Breasted Sunbird	0.050	-
Lesser Double Collared Sunbird	0.045	0.002
Cape Sugarbird	0.226	-
Malachite Sunbird	-	0.002
Cape white eyes	0.751	-
Fork-tailed Drongo	-	0.006
Cape Weaver	-	0.016
Apis mellifera (Honey Bee)	0.006	0.024
Tachypompilus ignitus & *Polistes* spp. (Wasps)	0.024	-

Supplementary Table 5. Climate model fit comprising four replicated models based on TSS and AUC values calculated for three model classes using ensemble forecasts.

Model Replicate	Model class	TSS	AUC
Mean	ANN	0.899	0.978
	GAM	0.910	0.989
	GBM	0.932	0.992
1	ANN	0.911	0.976
	GAM	0.907	0.988
	GBM	0.923	0.992
2	ANN	0.876	0.975
	GAM	0.909	0.991
	GBM	0.942	0.994
3	ANN	0.899	0.978
	GAM	0.902	0.989
	GBM	0.929	0.988
4	ANN	0.909	0.983
	GAM	0.920	0.991
	GBM	0.933	0.993

Supplementary Table 6. Current area occupied (convex hull polygons) and current and projected condensed hectares. Projections are for 2020 with the assumption of one fire occurrence during this time period.

	Waterford	Blomkloof (young)*	Blomkloof (old)	McGregor
Projected lower limit condensed hectares	21.28	2.46	0.94	1.23
Projected upper limit condensed hectares	118.79	13.04	7.82	8.86